ANALYSIS OF THE EASTWARD BREEDING EXPANSION OF BREWER'S BLACKBIRD PLUS GENERAL ASPECTS OF AVIAN EXPANSIONS

P. H. R. Stepney and Dennis M. Power

The present paper is part of a continuing study on ecological and evolutionary problems associated with the eastward range expansion of Brewer's Blackbird (*Euphagus cyanocephalus*). This recent expansion from western Minnesota to Sudbury, Ontario, a distance of approximately 700 miles, is believed by us to be due to individuals undergoing relocation from earlier nesting or wintering areas, and upon encountering recently created, favorable habitat east of where the species previously bred, establishing new breeding populations. Previously, Walkinshaw and Zimmerman (1961) reviewed all breeding and non-breeding records of this species east of the Mississippi River. The present study, in addition to updating information on the expansion of the breeding range within the Great Lakes region, analyzes the routes and rates of expansion, with thoughts on the phenomenon of expansion in general.

MATERIALS AND METHODS

The dates and locations of sightings within the expansion zone were obtained from the literature. Much of this information is summarized in one figure (Fig. 1, to be discussed beyond) which indicates year and locality of first known breeding birds or birds classed as summer residents, i.e. birds reported between 1 May and 31 July. The present map shows only those records pertinent to pioneering movements, although working maps showing nearly all records were originally produced. Symbols are used in the figure to indicate either nesting or summer residency. In cases where nesting was reported after an initial summer residency the symbol for nesting is used while the date refers to the earlier report of first residency. Normally only the first sighting per county is given, but in large counties or districts others may be given for clarification. In a few cases where the date of a report was the same as that of a neighboring report, the date is given only once. Where nest location was not specified we have plotted the symbol in the center of the county. References for dates in Figure 1 which are not given in this paper appear in Stepney (1971). The slightly modified boundaries of the potential vegetation shown in Figure 1 are after Küchler (1964). Figure 2, a representation of the routes followed, was constructed by connecting the areas with dates that indicated step-wise occupation. The rates of expansion given in Table 1 were determined by dividing the time between reports of invasion into the straight-line distance between the points of invasion.

PREVIOUS DISTRIBUTION OF BREWER'S BLACKBIRD

Prior to the 1900's, the Red River Valley in western Minnesota was the eastern distributional limit of Brewer's Blackbird (Coues, 1874). The species

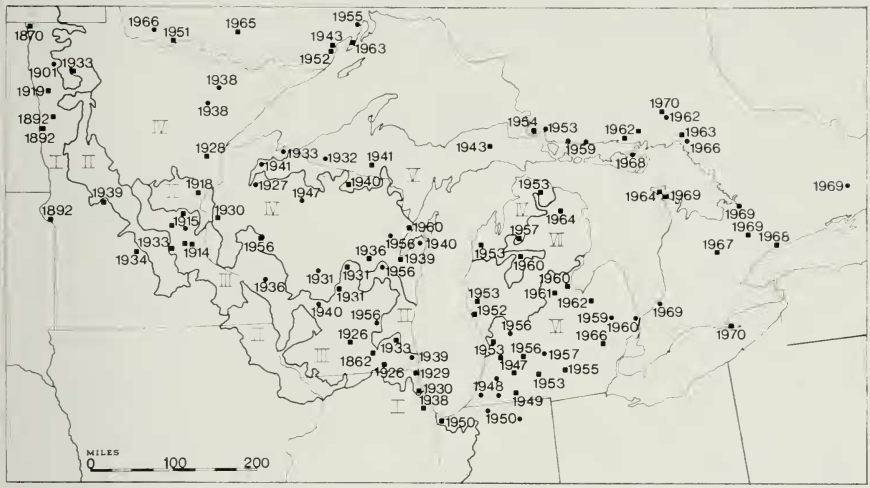

FIG. 1. Dates of sightings of Brewer's Blackbird and major vegetation types within the zone of expansion. Circles—summer resident, squares—known breeding. I—bluestem prairie, II—maple-basswood forest, III—oak-savanna cover, IV—Great Lakes spruce-fir and spruce-pine forest, V—northern hardwood-fir forest, VI—oak-hickory and beech-maple forest, VII—northern pine forest.

was recorded breeding in several western Minnesota counties, namely Kittson, Norman, Polk, and Big Stone Lake (Hatch, 1892). Occurrence farther eastward was probably restricted by the band of maple-basswood forest which paralleled the Red River Valley (Fig. 1) and then extended diagonally southeast across Minnesota and Wisconsin. By 1880 the forest had already been removed from the areas that the species was to later colonize in Minnesota and Wisconsin (Sargent, 1884), but expansion was delayed until the intervening maple-basswood forest barrier was destroyed about the turn of the century. With the removal of the barrier Brewer's Blackbird rapidly colonized the oak-savanna zone (Fig. 1), a vegetation belt the species had been recorded in five times prior to expansion (Kumlien and Hollister, 1903), but in which breeding populations had never become established.

Prior to expansion, numbers of Brewer's Blackbirds increased in the Red River Valley. The species became much more abundant in northeastern North Dakota around 1880 (Williams, 1926), and apparently commenced breeding in Marshall County in northeastern South Dakota sometime between 1870 and 1929 (Youngworth, 1935). There is insufficient information to determine if these changes resulted from an expansion originating farther westward or were just an increased occurrence in response to greater habitat availability resulting from agricultural activity. Youngworth (op. cit.)

supports the latter view. Whatever the cause, the increased density of Brewer's Blackbird probably assisted in launching the expansion into Minnesota.

DYNAMICS OF EXPANSION, ROUTES FOLLOWED

Expansion in Brewer's Blackbird appears to have been accomplished by single birds or small groups of individuals pioneering to what was presumably the nearest suitable area. Only in the Upper Peninsula of Michigan did the initial expansion movement appear to skip over an intervening area that was later colonized (Fig. 1). Although colonization (the first breeding in an area) and invasion (the first appearance in an area) often occurred concurrently, breeding was delayed in some areas. A delay of one to two years appears to have occurred in Walworth County, Wisconsin (Schorger, 1934), Port Arthur, Thunder Bay District, Ontario (Allin and Dear, 1947), Allegan County, Michigan (Walkinshaw and Zimmerman, 1961), Sault Ste. Marie, Algoma District, Ontario (Speirs, 1954) and Sudbury, Sudbury District, Ontario (Devitt, 1964). Unfortunately the ages of the pioneering individuals were not known. If the birds were juveniles, the case in many expanding species (Lack, 1954), then it is logical that breeding was delayed. Williams (1952) suggests that male Brewer's Blackbirds do not breed until their second year and preliminary observation of banded birds suggest the nestlings do not return to, or near, the parental area the following year. Age, however, is not the sole factor governing breeding, as these delays may have been due to poor habitat or too few individuals.

Within the expansion zone local populations have built up particularly around the centers of Minneapolis, Madison, Kalamazoo, Luce County, Michigan, Fort Francis, Port Arthur, Sault Ste. Marie, and Sudbury. These centers of occupation are presumably due to the increase of grassland habitat around centers of human habitation. The main habitat feature apparently necessary to induce settling is the presence of sufficient area offering little vegetational hindrance to movement while foraging (Stepney, 1971). In forest zones, the production and maintenance of suitable foraging areas are dependent upon human activity. Consequently, Brewer's Blackbirds are closely associated with farmlands, towns, highway and railway rights-of-way.

Inspection of dates of first breeding or summer occurrence (Fig. 1) allows determination of the most probable routes of expansion eastward (Fig. 2). (For reasons we will develop beyond, we have considered expansion from one breeding area to the next, rather than from the wintering grounds). The initial expansion into Minnesota was along only one route although several distinct routes ultimately developed within the remaining expansion zone. The initial expansion occurred into central Minnesota where the species was found breeding at Minneapolis in 1914 (Roberts, 1914). From here the

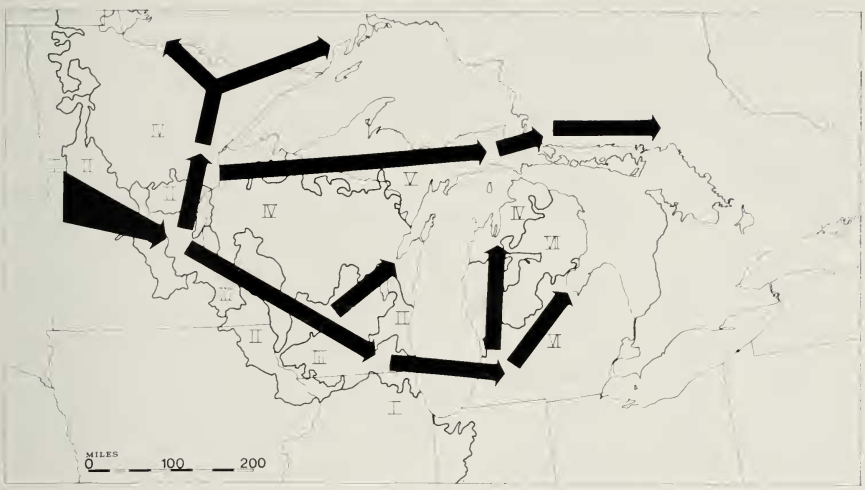

FIG. 2. Inferred expansion routes of Brewer's Blackbird.

blackbird penetrated farther east, reaching Madison, Wisconsin in 1926 (Schorger, 1934). Two northward routes then developed from this initial eastward extension. The more important route was observed in 1928 when the species was found breeding in the less modified areas of the Great Lakes Forest north of Minneapolis (Roberts, 1932). The second northward turning took place near Madison, where the species again invaded the forest but penetrated only as far as the Green Bay, Wisconsin area.

The route north from Minneapolis soon divided; one branch continued northward through Minnesota and the other moved east across the Upper Michigan Peninsula. The route through northern Minnesota again divided, with one terminus reaching Port Arthur, Ontario by 1943 (Allin and Dear, 1947) and the other extending northwest, reaching Fort Francis, Ontario by 1951 (Baillie, 1961). The invasion across the Upper Michigan Peninsula proceeded rapidly reaching Luce County, Michigan by 1943 (Walkinshaw and Zimmerman, 1961). From Luce County the species moved into the Sault Ste. Marie, Ontario area by 1953 (Speirs, 1954), then continued eastward reaching Sudbury, Ontario by 1962 (Devitt, 1964). A minor southward extension developed from the Sudbury route but appears not to have persisted. There has been one report of summer residents on Manitoulin Island (Power, 1971) and two reports of breeding birds in the Bruce Peninsula (Goodwin, 1969) but no subsequent sightings from either area have been reported.

The remaining expansion route was the colonization of Kalamazoo, Michigan from the Madison, Wisconsin area observed in 1947 (Fleugel, 1948).

From Kalamazoo two extensions developed. The first was a southwestward movement into northwestern Indiana by 1950 (Mumford, 1954). The complete sequence of dates from Kalamazoo, Michigan to Gary, Indiana (Fig. 1) and the absence of Brewer's Blackbird from the Chicago area, suggest expansion occurred across rather than around Lake Michigan. The second expansion from Kalamazoo went north along Lake Michigan, the species reaching Benzonia by 1953 (Walkinshaw and Zimmerman, 1961) and Bay City by 1960 (Kenaga, 1961). Another possibility is that parts of northern Lower Michigan, particularly Cheboygan County were colonized via Luce County in Upper Michigan. Owing to the ambiguity of the data we have chosen Kalamazoo as the source region for the Lower Michigan expansions, as it is the least circuitous. To date the distribution of Brewer's Blackbird within the expansion zone is still strongly influenced by these original expansion routes. Overall, the occurrence and numbers of Brewer's Blackbirds tend to decrease moving both north and east in the expansion zone.

Expansion into southeastern Lower Michigan and southern Ontario has not occurred, although a few isolated nestings have been reported (Devitt, 1969; Poitter and Hirt, 1966; Richards and Peck, 1968). The failure of Brewer's Blackbird to establish permanent breeding populations in these areas may be a result of competitive overlap with the Common Grackle (*Quiscalus quiscula*) (Stepney, 1971), an icterid with somewhat similar ecological requirements and one which becomes very abundant in southeastern Lower Michigan and eastward (Zimmerman and Van Tyne, 1959).

The pattern of dates suggests that expansion may have been accomplished primarily by the relocation of surplus individuals to suitable habitat which is nearest to the previously occupied breeding areas. Although occupation of new areas could also have been accomplished through direct movement from the wintering range, this alternative viewpoint seems less attractive, primarily because a number of more northern areas were occupied before southern ones. For example, parts of Upper Michigan were colonized before Lower Michigan, and within Lower Michigan, breeding colonies had become established in the northern section before much of the southern section was colonized.

EFFECTS OF BARRIERS UPON THE RATE OF EXPANSION

Disregarding the initial forest barrier, five major vegetation zones were colonized by Brewer's Blackbird while moving eastward (Fig. 1). On three occasions water barriers of appreciable magnitude were encountered. Expansion across vegetation-zone boundaries or water barriers was at a slower rate than was expansion within a given vegetation zone or before and after overcoming a water barrier (see Table 1). Water barriers hampered expansion more than vegetational barriers but neither exerted more than a temporary

TABLE 1

RATES OF EXPANSION BETWEEN VARIOUS CENTERS AND THE DISTANCES AND TIMES INVOLVED

Pioneering Movements	Distance (miles)	Time (years)	Theoretical Expansion Rate (miles per year)
a. minor			
Minneapolis to Madison	277	12	23.0
Madison to Kalamazoo	77	21	3.6
Minneapolis to western Lake Superior	110	14	7.8
Western Lake Superior to Fort Francis	170	23	7.3
Western Lake Superior to Thunder Bay	236	15	15.3
Western Lake Superior to Luce Co., Michigan	315	16	19.7
Luce Co., Michigan to Sault Ste. Marie	69	10	6.9
Sault Ste. Marie to Sudbury	154	9	17.1
b. major			
Minneapolis to Kalamazoo	354	33	10.1
Minneapolis to Thunder Bay	346	29	11.9
Minneapolis to Fort Francis	280	37	7.5
Minneapolis to Luce Co.	452	30	14.1
Minneapolis to Sudbury	648	49	11.1
c. *general expansion rate*	10.9 miles per year		

restraint. In addition, the suitability and availability of grassland habitat within each vegetational region were likely responsible for variation in expansion rates. The oak-savanna vegetation belt was colonized most rapidly presumably because it was the area physiognomically most similar to the areas west of Minnesota. For example, the stretch of oak-savanna vegetation from Minneapolis, Minnesota to Madison, Wisconsin was colonized at a rate of about 23 miles per year. Conversely, the expansion north through forested areas was at a lower rate, particularly into the Fort Francis area where the availability of suitable habitat was reduced. For this area colonization from western Lake Superior to Thunder Bay, Ontario was at about 15 miles per year and from western Lake Superior to Fort Francis, Ontario was at only 7 miles per year.

Expansion beyond the oak-savanna zone was accomplished three times by crossing a vegetational barrier and once by crossing a water barrier (Figs. 1 and 2). The rates of invading the Great Lakes Forest north of Minneapolis and Madison were reduced to one-third and one-fifth, respectively, of the rate demonstrated while colonizing the oak-savanna region. The bluestem prairie, the habitat type originally occupied in western Minnesota, was

reinvaded south of Madison, but at only one-quarter the rate of the oak-savanna expansion. The cause of this anomaly is uncertain. The only water barrier encountered when expanding from the oak-savanna region was Lake Michigan. Expansion across the Lake was slowest of all, presumably due to the magnitude of the barrier.

The route into the forested area north of Minneapolis was the most important of the expansions from the oak-savanna region. After initial slowing while crossing the vegetational boundary (Table 1, Minneapolis to western Lake Superior at 8 miles per year), the rate increased more than two-fold during expansion into Thunder Bay. However, the rate remained about the same while expansion to Fort Francis was underway. Presumably this reflects the differences in the availability of habitat along the two routes, the Fort Francis route having fewer areas where the forest has been disturbed.

A rate increase to 20 miles per year across the Upper Peninsula of Michigan was greater than the increase on the Thunder Bay route. The rate of expansion was presumably enhanced by more extensive habitat modification and the presence of natural treeless regions in the counties of Marinette, Schoolcraft, and Luce (Sargent, 1884). These treeless areas are coincident with the earliest centers of colonization (Fig. 1). From Luce County expansion both east and south of the peninsula was seemingly hampered by water barriers and perhaps poor habitat. Expansion eastward across the Soo Canals slowed to 7 miles per year, one-third the previous rate, and east of the Canals increased again to 17 miles per year, a rate similar to that of expansion across the Upper Michigan Peninsula. The Straits of Mackinac may have stopped expansion from the Upper Michigan Peninsula into Lower Michigan entirely, as discussed previously. However, if Cheboygan County was colonized by movement across the Straits of Mackinac, the rate slowed to 8 miles per year, again reflecting the slowing effect of a water barrier.

The expansion rates along the principal routes reflect the influence that the extent of modification and the number and magnitude of barriers encountered have had upon each local extension. The data suggest that the species is not an innate disperser, that is, tending to make relatively sudden, long-distance expansion movements (Howard, 1960). Rather it is suggested individuals expand only until an area suitable for occupation is located. Environmentally induced dispersal (Howard, op. cit.) by Brewer's Blackbird is also supported by the slowing effect unfavorable habitat or barriers have upon expansion (i.e. the Fort Francis route) in contrast to the innately dispersing Starling and House Sparrow which, upon encountering unfavorable habitat in parts of North America, experienced an increase in the rate of expansion (Wing, 1943).

DISCUSSION

The eastward expansion of Brewer's Blackbird appears to be due to the production of suitable habitat in what was previously a forested area. Although much of this newly created habitat was available approximately 40 years prior to colonization, expansion did not occur until there was a population build-up in western Minnesota, the previous eastern limits of the species distribution. Once expansion started, invasion appeared to be accomplished by the environmental displacement of surplus individuals. With each displacement the individual birds appeared to select the most suitable habitat geographically nearest to the previous breeding center. As the production and maintenance of suitable habitat within the Great Lakes region is dependent upon human activity, the expansion soon divided into three major routes as the birds followed the principal roadways and railroads linking centers of human activity.

During expansion, water and changes in vegetational cover acted as the main barriers to movement. Although both types of barriers proved to be only temporary, bodies of water had a greater retarding effect. The apparent cessation of the overall eastward expansion appears to be due to increasing amounts of competitive overlap with the Common Grackle, particularly where this species increases in density. A study of abundance and distribution of these two species supports this view (Erskine, 1971). These aspects, however, are to be discussed in detail in a paper now in preparation.

In the eastward expansion of the breeding range of Brewer's Blackbird we see a rather orderly progression with moderate expansion rates within a particular vegetation type and lower expansion rates where new vegetation types or geographical barriers are encountered. In fact this has led us to describe the expansion as movement from one nesting locality to another when in reality the species is migratory and could be moving to new breeding sites directly from the wintering grounds, which have also changed in recent years (Stepney, 1971). We have no firm evidence one way or the other on this point, but because of the rather orderly progression eastward we documented expansion from one breeding area to the next whether the birds are behaving exactly in this way or not.

This pattern of a gradual, dendritic movement eastward fits in with the fact that Power (1971) did not find differences in phenetic variability in a new eastern population of Brewer's Blackbird. In Power's study there were no tendencies for variances in skeletal and external characters to be larger or smaller in a population near McKerrow, Ontario, established in 1962 (samples were taken in 1968) when compared to a sample from Winnipeg, Manitoba. An increase in variability would have been expected if expansion had resulted from a sudden population flush, while, on the other hand, a decrease ("founder

effect") would have been expected had colonization been due to establishment of nesting colonies by just a few individuals that remained reproductively isolated from populations to the west.

THOUGHTS ON RANGE EXPANSIONS

In the following discussion we have attempted to synthesize a generalized framework for the phenomenon of range expansions.

The distributional limits of a species are probably always in a state of flux. Occasionally relatively rapid changes, which we commonly term "range expansions," take place over a few years or decades and provide the opportunity for study. We define a range expansion as the relatively rapid establishment of a regularly recurring breeding or wintering population beyond some prior distributional limit.

The potential for annual expansion may always exist, coincident with post-breeding season increases in population. The common appearance of individuals beyond their normal breeding range suggests that species frequently occur beyond the edge of their ranges without establishing permanent populations (for example, see Parslow, 1967; 1968). A true range expansion appears dependent upon factors which once excluded a species from an area being removed or altered.

Certain features appear to be common to most range expansions, particularly continental expansions (see Mayr, 1965, for a discussion of expansions by island faunas). The initial invasion, except when eruptions result in short-lived extensions (Cornwallis, 1961), generally involves low numbers of individuals, many of which are juveniles (Lack, 1954). It also appears to us that expansions follow one of three basic patterns. The first pattern involves explosive movement, birds radiating outward in several directions, initially colonizing many isolated points. The gaps between colonizing centers, if suitable, are occupied at a later date.

The second pattern of expansion may be described as dendritic. Species demonstrating this pattern expand in a more step-wise manner along routes which are distinct in at least the early stages of expansion. Colonization centers are generally not far apart but individual routes may extend an appreciable distance outward from the previous distribution. Invasions of this nature appear to be undertaken by a few individuals and breeding occurring concurrently with invasion or within approximately three years.

The third pattern of expansion is the least dynamic. It involves a slow movement along a rather continuous population front, breeding almost always occurring during the year of invasion.

Examples of various range expansions by species in North America and Europe which demonstrate these three basic patterns may be found in Beddall

(1963), Kalela (1949), Keve (1963), Lack (1971), Odum and Burleigh (1946), Odum and Johnston (1951), Rice (1956), and Wing (1943).

These expansion patterns are suggested to be related to two broad groups of factors, grouped according to whether they operate primarily independently of the species' activity or not. Extrinsic, or independent, factors affecting expansion would include climate, predators, parasites, habitat quality and availability, plus the extent to which other members of the avifauna may directly or indirectly interfere with the species. Ordinarily such extrinsic factors would work against expansion resulting in a stable distribution. Intrinsic factors, those associated with the species' life history, would consist of factors such as the type of dispersal, population density and age structure, natural rate of increase, physiological tolerance, nature of inter-individual spacing, and the amount of ecological variability demonstrated by the species. These intrinsic factors normally exert outward pressure upon the limits of distribution. That range expansions occur infrequently is due, presumably, to the total effect of the extrinsic factors normally being greater than the intrinsic factors. The relative importance of the various factors within each category presumably differs between species and to a lesser extent between populations.

Although expansions may result from various combinations of the suggested causal factors, certain factors appear to be rather consistently associated with one particular expansion pattern. Explosive patterns are commonly associated with the species suddenly gaining access to large tracts of suitable habitat either by the recent appearance of the new area of habitat or through the surmounting of a previous barrier, by natural or assisted means. High dispersal rate, an intrinsic factor, also favors an explosive expansion. A dendritic expansion is commonly associated with new areas of habitat occurring only in limited areas and is commonly seen in species which are able to take advantage of areas highly modified by human activity. This is particularly applicable to species requiring an "edge effect" (Odum and Burleigh, 1946). The factors commonly associated with slow, wide-front, expansions are climatic shifts (Udvardy, 1969), ecological succession (Johnston and Odum, 1956) and wide-scale community alterations.

SUMMARY

Within the last 60 years Brewer's Blackbird has expanded its breeding range approximately 700 miles into the Great Lakes region. Its distribution has increased through the creation of suitable habitat resulting from forest removal by man.

Three principal routes were followed eastward through the expansion zone, these routes giving rise to several of lesser magnitude. Expansion originated in western central Minnesota. From there one route went northward and west of Lake Superior, a second went

eastward between Lake Superior and Lake Michigan and a third moved through central and southern Wisconsin across the southern end of Lake Michigan.

The rates of expansion along the routes varied according to the extent of habitat modification and the presence of vegetational and aquatic barriers. Five vegetational and three aquatic barriers were encountered. Although aquatic barriers had a greater effect upon the expansion rate, both types of barriers only slowed expansion temporarily. The average expansion rate through the Great Lakes region has been 11 miles per year.

In general the potential for range expansion is suggested to exist annually, the impetus being derived primarily from post-breeding dispersal activity and other species-dependent activity. However, a host of factors which operate independently of a species' biological activity continually work against expansion. Only with the alteration of one or more of the constraining factors is an expansion possible. Range expansions appear to demonstrate three basic patterns; an explosive pattern, a dendritic pattern, or a slow, even-front pattern. Each pattern is commonly associated with one or two specific constraining factors whose alteration has enabled the species to expand. The difference between expansion patterns is also particularly affected by the type of dispersal activity exhibited by the species.

In Brewer's Blackbird, eastward expansion of the breeding range appears as a continually growing dendritic pattern along recently produced tracts of grassland habitat. The species is not characterized by any particular innate characters which promote sudden increases in numbers and range.

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF TORONTO, TORONTO, ONTARIO AND DEPARTMENT OF ORNITHOLOGY, ROYAL ONTARIO MUSEUM, DEPARTMENT OF ZOOLOGY, UNIVERSITY OF TORONTO, TORONTO, ONTARIO (PRESENT ADDRESS: DMP, MUSEUM OF NATURAL HISTORY, 2559 PUESTA DEL SOL ROAD, SANTA BARBARA, CALIFORNIA 93105, 1 NOVEMBER 1972).

NEW LIFE MEMBER

Dr. Oliver H. Hewitt has recently become a Life Member of The Wilson Society. Dr. Hewitt is Professor Emeritus of Wildlife Science at Cornell University, and is presently a Research Associate at the Mote Marine Laboratory, Sarasota, Florida. He holds degrees from McMaster University and Cornell University. His interests in ornithology are in population measurement, marine birds and waterfowl, and he has over 50 publications in ornithology, as well as serving as editor of the monograph on the Wild Turkey published by The Wildlife Society. He is a member of the AOU, The Littoral Society, American Society of Mammalogists, and The Wildlife Society which he served as a Vice-President and as Editor of *The Journal of Wildlife Management.*

Dr. Hewitt lists his hobbies as scuba diving, photography, and boating, and tells us that he has three daughters (all married).